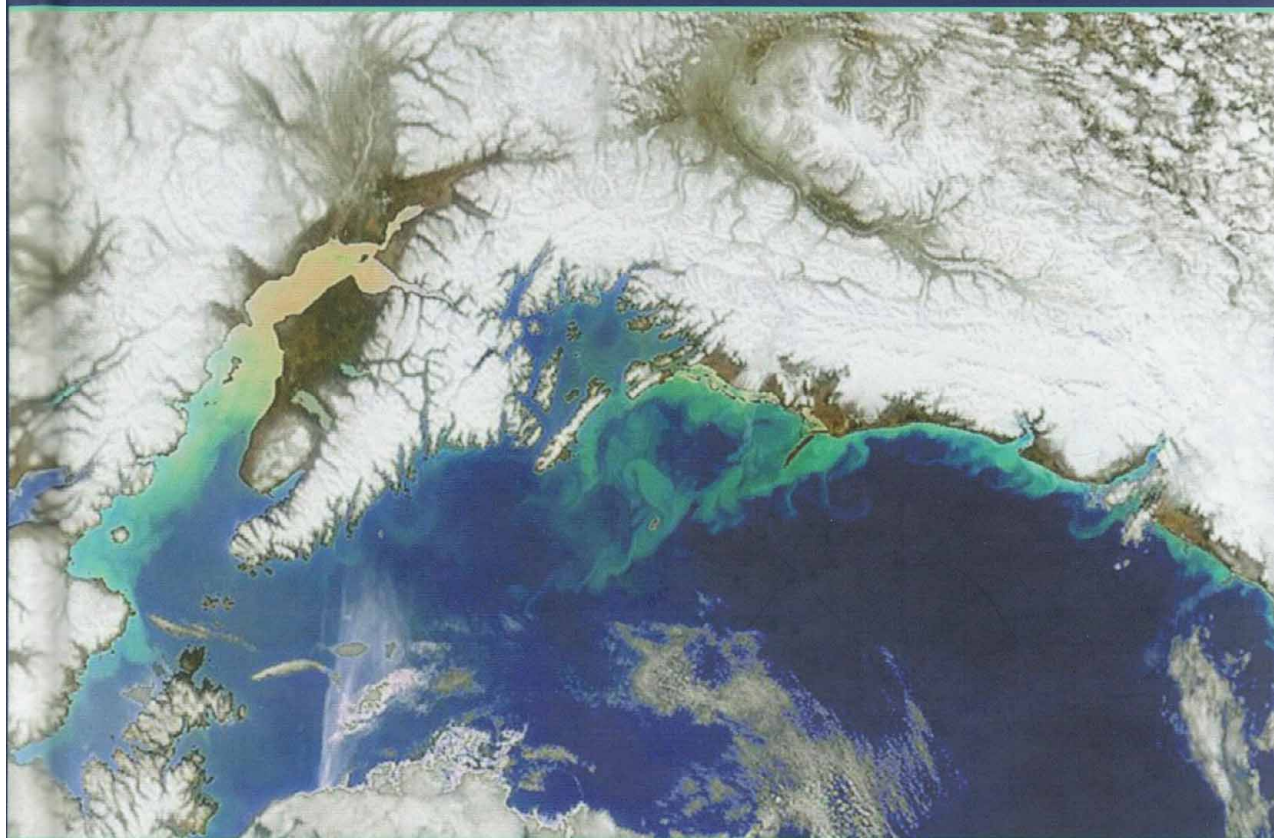


Long-Term Ecological Change in the Northern Gulf of Alaska



ROBERT B. SPIES EDITOR

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4.8. Population Ecology of Seabirds in Cook Inlet

John F. Piatt and Ann M.A. Harding

4.8.1. Introduction

Many seabird colony populations in the Gulf of Alaska have fluctuated in recent decades, and they have declined markedly at a few sites (Hatch and Piatt, 1995; Dragoo et al., 2000). The *Exxon Valdez* oil spill of 1989 had an immediate impact on some seabirds (Piatt et al., 1990; Piatt and Ford 1996), adding to other anthropogenic factors influencing seabird populations in Alaska (e.g., gill-net mortality, introduced predators, etc.; Hatch and Piatt, 1995). However, evidence accumulated during the 1990s that background variability in the marine environment had an even greater effect on seabird populations over annual and decadal timescales. Most notably, a “regime shift” occurred in the Gulf of Alaska during the late 1970s, apparently causing marked changes in seabird diets, lower reproductive success, occasional wrecks (large-scale die-offs), and long-term declines in some marine bird and mammal populations (Piatt and Van Pelt, 1997; Piatt and Anderson, 1996; Francis et al., 1998). Fish communities on the continental shelf of the Gulf of Alaska also changed dramatically during that time period (Anderson and Piatt, 1999). Coincident with cyclical fluctuations in seawater temperatures, the abundance of small forage fish species such as capelin (*Mallotus villosus*) declined precipitously in the late 1970s, while populations of large predatory fish such as walleye pollock (*Theragra chalcogramma*) and

cod (*Gadus macrocephalus*) increased dramatically. Correspondingly, capelin virtually disappeared from seabird diets in the late 1970s, and were replaced by juvenile pollock and other species in the 1980s (Piatt and Anderson, 1996). Seabirds and marine mammals exhibited several signs of food stress (population declines, reduced productivity, and die-offs) throughout the 1980s and early 1990s (Merrick et al., 1987; Piatt and Anderson, 1996).

In part because of these observations, the *Exxon Valdez* Oil Spill Trustee Council initiated the Apex Predator Ecosystem Experiment (APEX) in 1994 to assess whether post-spill environmental conditions could influence the recovery of seabirds from the oil spill. Initially focused on Prince William Sound, APEX studies expanded in 1995 to include Cook Inlet, where it was possible to conduct seabird and forage fish studies around three seabird colonies (Chisik, Gull, and Barren Islands) (Fig. 4.37). Oceanography, plankton, forage fish ecology, and seabird distribution at sea were studied in waters around each colony (Drew, 2002; Drew and Piatt, 2002; Piatt, 2002a; Robards et al., 1999a,b,c; Robards, 2000; Robards et al., 2002; Abookire et al., 2000; Abookire and Piatt, 2004; Litzow et al., 2000; 2004a,b, Speckman, 2004;

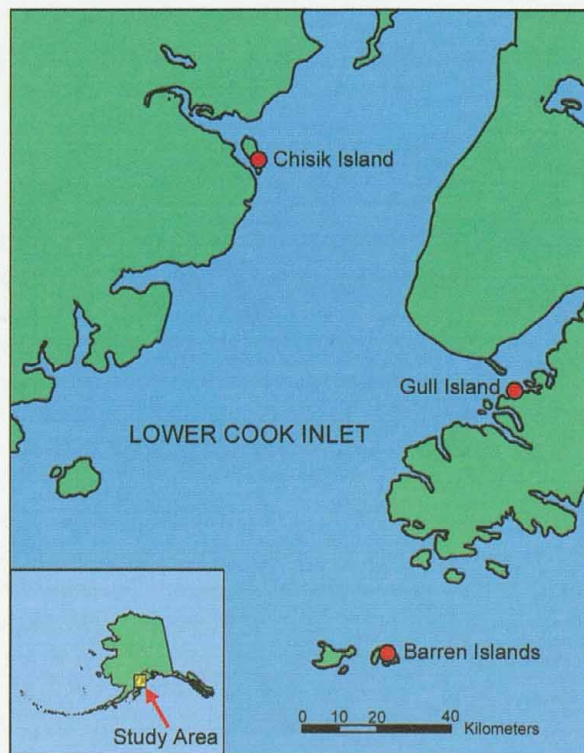


Figure 4.37: The location of the three study colonies in lower Cook Inlet.

Speckman et al., 2005). Seabird foraging behavior, diets, time budgets, chick growth rates, physiological condition, reproductive success, population trend, and adult survival were studied concurrently at each of the three colonies (Roseneau et al., 1997, 2000; Zador et al., 1997; Kitaysky et al., 1998, 1999, 2001, 2005; Piatt et al., 1999; Zador and Piatt, 1999; Litzow, 2000; Litzow et al., 2000; Romano, 2000; Van Pelt, 2000; Harding, 2001; Harding et al., 2002, 2003; Litzow and Piatt, 2003; Piatt, 2004). Most data were collected on common murre (*Uria aalge*; Van Pelt et al., 2002) and black-legged kittiwakes (*Rissa tridactyla*, Shultz et al., 2002), which breed at all three study sites in lower Cook Inlet.

Results of APEX work are still being published, but here we summarize some of the main findings of studies in lower Cook Inlet. After a brief review of the Cook Inlet ecosystem, we consider some of the similarities and differences in the way murre and kittiwakes respond to fluctuations in food supply. We then consider murre and kittiwake population dynamics in Cook Inlet and elsewhere in Alaska and what this may reveal about long-term changes in the marine environment of the Gulf of Alaska and Bering Sea.

4.8.2. The Cook Inlet Ecosystem

We set out from the beginning to study seabirds and prey resources at colonies known from historical work to be chronically failing (Chisik Island), thriving (Gull Island), and possibly stable or recovering from the oil spill (Barren Islands). Our hope was that historic differences in bird biology were indeed the result of regional differences in food supplies and that, by studying all three colonies for five years, we would obtain enough data to characterize favorable and unfavorable environmental settings for seabirds (Piatt, 2002b).

The engine that drives productivity in lower Cook Inlet is the persistent upwelling of cold, nutrient-rich water at the entrance to Cook Inlet (Fig. 4.38). A plume of cold Gulf of Alaska water that extends from the Barrens to Kachemak Bay (large bay on the east side of lower Cook Inlet) persists throughout summer in all years (Drew and Piatt, 2002; Speckman et al., 2005) and provides nutrients that fuel extraordinary primary production (Drew, 2002). Waters on the west side of lower Cook Inlet are oceanographically distinct (warmer, less saline, weakly stratified, turbid, and outflowing), and much less productive. The east–west difference in oceanography and primary production is reflected at all higher trophic levels. The abundance of zooplankton (Drew, 2002; Speckman et al., 2005), forage fish offshore (Abookire and Piatt, 2004; Speckman, 2004) and nearshore (Robards et al., 1999b), and seabirds (Speckman, 2004) is in all cases 1–2 orders of magnitude greater on the east side of lower Cook Inlet. The growth rate of resident forage fish such as sand lance (*Ammodytes hexapterus*) is significantly lower in Chisik waters than in Kachemak Bay

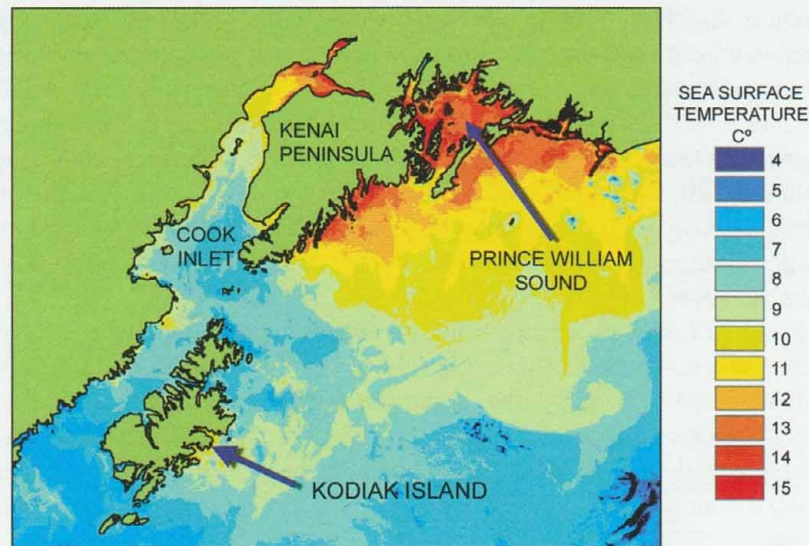


Figure 4.38: Sea surface temperature in the northern Gulf of Alaska on July 3, 1999. Note the colder (blue) surface water that results from upwelling in lower Cook Inlet and east of Kodiak Island in contrast to the warmer (red–orange–yellow), stratified waters in Prince William Sound and shelf waters south of the Kenai Peninsula. Data is from NOAA AVHRR satellite.

(Robards et al., 2002). Thus, all evidence suggests that lower Cook Inlet is segregated into distinct oceanographic domains, with striking differences in productivity and biology among them (Speckman et al., 2005).

In all years, the well-mixed, cold waters in the lower inlet – particularly offshore – were dominated by juvenile pollock and capelin (Abookire and Piatt, 2004), important prey for murre (Van Pelt et al., 2002). Sand lance and herring (*Clupea pallasii*) were the most common prey for kittiwakes (Shultz et al., 2002), and were most abundant in stratified coastal waters of the Kenai Peninsula and Kachemak Bay (Robards et al., 1999b; Abookire and Piatt, 2004). Fish were markedly variable in the vertical dimension as well. Most acoustic biomass was concentrated in the upper 30 m in all areas, but in Chisik and Barren island waters, schools were also concentrated at depths of 60–100 m (Speckman, 2004). There was also a clear segregation of species by water depth; sand lance and herring dominated above depths of 40 m, whereas pollock and capelin dominated below 60 m.

Diets of adult murre and kittiwakes reflected food supplies around each colony. Whereas more than 90 species of fish were caught near shore and 40 species were caught in offshore trawls, communities were overwhelmingly dominated (>95%) by

four species: sand lance, herring, Pollock, and capelin (Robards et al., 1999b, 2002; Abookire and Piatt, 2004). Diets of adult murres and kittiwakes were dominated by the same species in similar proportions to local abundance except that herring were generally eaten less and capelin eaten more in proportion to their relative abundances (Van Pelt et al., 2002; Shultz et al., 2002). Sand lance dominated murre and kittiwake diets at both Chisik and Gull, while pollock comprised a much larger proportion in diets of birds from the Barrens. The size classes of prey eaten by adults was similar to the size classes caught in trawls and seines. Taken together, the evidence suggests that adult murres and kittiwakes generally eat what is most available to them within foraging range of their colonies. In contrast to adult diets, however, chick diets were poor indicators of relative prey availability because adults choose to feed their chicks prey that are oily and rich in calories, a behavior with obvious adaptive value.

The breeding biology of seabirds differed markedly among colonies owing to the persistent geographic differences in forage fish availability described earlier. Birds at Chisik Island struggled to reproduce, while those at Gull and Barren islands usually had few problems rearing young (Kitaysky et al., 1998, 1999; Zador and Piatt, 1999; Shultz et al., 2002; Van Pelt et al., 2002). Within each colony, breeding and behavioral parameters varied among years to a lesser degree than among sites. Breeding success in all species was lower in 1998 than in other years; presumably a lingering effect of the previous winters' El Niño event (Piatt et al., 1999). Population censuses revealed that seabirds at Chisik Island continued in a long-term decline, whereas populations at Gull and Barren islands were increasing (Zador et al., 1997; Roseneau et al., 1997, 2000; Piatt, 2002a). Behavioral studies revealed that seabirds worked harder (longer foraging trips, less discretionary time) at colonies where nearby fish densities were lower (Zador and Piatt, 1999; Piatt, 2002a).

Overall, the studies show that seabird parameters (breeding success, foraging effort, population trend, etc.) varied most between islands and to a much lesser degree between years. We attribute this regional variability and temporal stability in seabird biology to distinct, persistent oceanographic regimes around each colony that determined the availability of fish to birds within those areas (Abookire and Piatt, 2004; Speckman et al., 2005).

4.8.3. Response of Seabirds to Variability in Prey

Form of Response

We predicted that – just like other vertebrates (Holling, 1959; Murdoch and Oaten, 1975; Piatt, 1990) – murres and kittiwakes would exhibit nonlinear functional relationships with food supply (Piatt, 2002b). Of the 25 relationships that we examined between parameters of seabird biology, behavior or physiology e.g., clutch size,

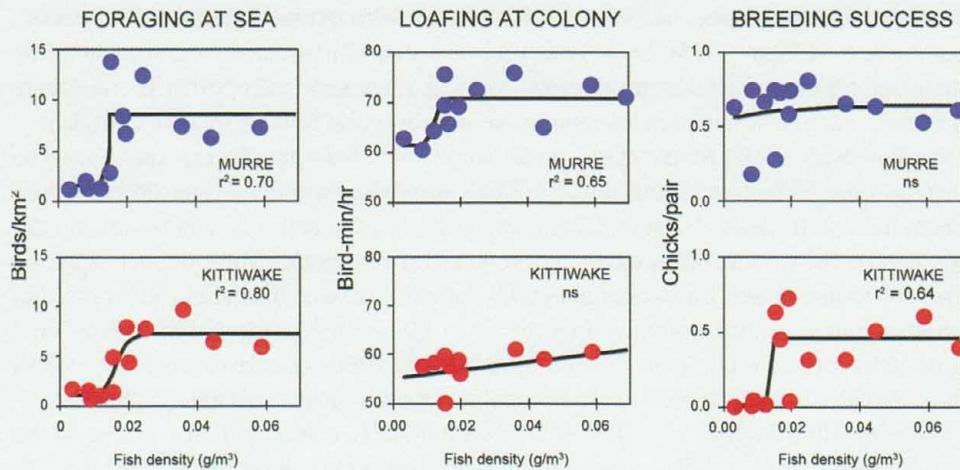


Figure 4.39: Behavioral and reproductive responses of common murre and black-legged kittiwake to variation in their food supply.

body condition, chick growth, hatching success, feeding rate, etc.) and prey density, more than half (14) were nonlinear, only one was linear, and the rest were not described by any significant model (Piatt, 2002a). For example, the attraction of foraging murres and kittiwakes to prey schools at sea (the “aggregative response”) was sigmoidal for both species (Speckman, 2004) (Fig. 4.39).

In recent years, breeding success in several seabird species has been shown to be a curvilinear function of food density (Arctic skua, Philips et al., 1996; Atlantic puffin, Anker-Nilssen et al., 1997; Arctic tern, Suddaby and Ratcliffe, 1997), and we demonstrated a similar relationship for black-legged kittiwakes (Fig. 4.39). Common murres did not exhibit such a relationship because breeding success was usually buffered by the ability to increase time spent foraging in the face of declining food supply. Instead, we observed a curvilinear relationship between discretionary time spent at the colony and food density in murres (Fig. 4.39). These and other functional response curves in murres and kittiwakes (Piatt, 2002a) suggests that food supplies at Gull and Barren islands – but not at Chisik – are above threshold limits and adequate to support recovery of losses from the *Exxon Valdez* oil spill.

Variability in Response

We found that neither hatching, fledging, nor breeding success in common murres was correlated with food supply (Shultz et al., 2002; Piatt, 2002a). Murres appeared to have trouble fledging chicks in only 2 of 14 colony-years of study (Fig. 4.39). On these two occasions, murres exhibited unusually low hatching success (52% vs.

70–90%), fledging success (<45% vs. 64–92%), and consequently low overall breeding success (<30% vs. 53–81%). In other years, however, murres were never limited by food supplies. It appears that they were able to compensate for low food abundance by reducing time spent attending their nest site (Fig. 4.39) and devoting that time to foraging (Burger and Piatt, 1990; Zador and Piatt, 1999). Because of this buffering capacity, murre fledging success (CV = 28%), and breeding success (CV = 29%) were about three times less variable than kittiwake fledging success (CV = 81%) and breeding success (CV = 87%) during 14 colony-years of study in Cook Inlet (Piatt, 2002a).

Despite a robust capacity to deal with variation in prey abundance, however, murre breeding success cannot be completely independent of food supply. Functional response curves for *aggregation* and *discretionary time* spent at the colony (Fig. 4.39) indicate that murres – as with kittiwakes – have a foraging threshold at about 0.013 g/m³ of fish biomass. Perhaps we failed to characterize a functional *reproductive* response curve because food supplies were never so low that they could not be behaviorally buffered to prevent breeding failure. Consequently, while we frequently observed kittiwake breeding failures in Cook Inlet, we never observed total breeding failure in murres. One explanation for the difference may be that when they are faced with the same prey fields around a colony, murres can fly further and search nearly twice as much surface area than kittiwakes in the same time, dive far below the surface in search of prey, and they have more discretionary time to divert to foraging (Piatt, 2002a).

How representative are these data from Cook Inlet for murres and kittiwakes elsewhere? We can examine variability in breeding success of murres and kittiwakes from long-term (1975–1999) data collected throughout Alaska (Gulf of Alaska, Aleutians, Bering, and Chukchi Seas) in a variety of monitoring and research programs (Hatch et al., 1993; Dragoo et al., 2000). From these data (Fig. 4.40, Table 4.4), which include an extreme – but natural – range of environmental conditions for breeding (Hatch et al., 1993), we find that common murres ($n = 14$ colonies, $n = 99$ colony-years) have rarely exhibited complete breeding failure (0 chicks/pair on only 4% of occasions), and on only 26% of the occasions was breeding success indicative of a limiting food supply (i.e., below 0.40 chicks/pair; see earlier text). Remarkably, common murres were successful (>0.40 chicks/pair) about three-quarters of the time (Fig. 4.40) and variability in breeding success was quite low (CV = 40%) and similar to that observed in Cook Inlet (CV = 28%). In contrast, kittiwakes ($n = 17$ colonies, $n = 235$ colony-years) had complete failures (0 chicks/pair) 18% percent of the time, and showed signs of food limitation (breeding success <0.46 chicks/pair) 77% of the time. On only 23% of occasions did kittiwakes appear to be unrestricted by food supply. Kittiwakes showed high levels of variability in breeding success in Cook Inlet (CV = 87%) and Alaska (CV = 110%).

A similar contrast in murre and kittiwake breeding success has been noted elsewhere (Table 4.4). Common murres observed during 54 colony-years at a variety of

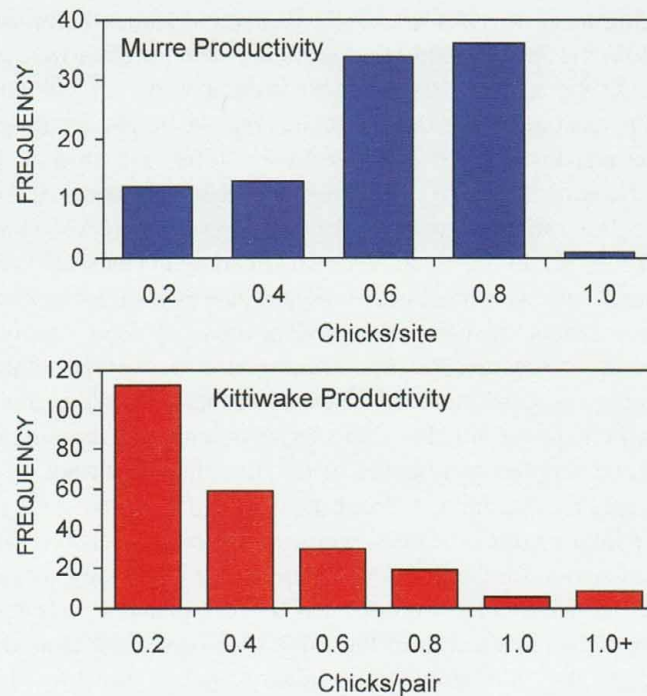


Figure 4.40: Frequency of different levels of breeding success for common murre and black-legged kittiwakes in Alaska (data from Hatch et al., 1993; Dragoo et al., 2000; Roseneau et al., 2000; Piatt, 2002a). Values are the upper end of the range, i.e., 0.2 is the frequency of breeding success between 0 and 0.2 chicks per pair. The murre graph includes 96 colony-years of data, and the kittiwake graph includes 232 colony-years, where a colony-year comprises data collected at any one colony in 1 year.

colonies in the North Atlantic (Birkhead, 1976; Hedgren, 1980; Birkhead and Nettleship, 1987; Harris and Wanless, 1988, unpublished data; Burger and Piatt, 1990; Bryant et al., 1999) averaged 0.75 ± 0.09 S.D. chicks/pair. Despite the span of years (1963–2001) and colonies ($n = 11$), variability in breeding success was low ($CV = 12\%$), with only one occasion where breeding success was less than 0.4 chicks/pair (0.26 chicks/pair, remaining values ranged from 0.52–0.88 chicks/pair). At the Isle of May, murre never failed in 21 years of study (range 0.63 to 0.81 chicks/pair; M. Harris and S. Wanless, unpublished data). Likewise, in 29 years of study at the Farallon Islands, California, common murre failed (<0.4 chicks/pair) only three times, all in association with strong El Niño (ENSO) events (Sydeman et al., 2001). Otherwise, breeding success ranged between 0.61 and 0.91 chicks/pair.

Table 4.4: Variability in breeding success of black-legged kittiwakes and common murre in different geographic areas.

Species	Location	Breeding Success			
		N (years)	mean	CV (%)	S.D.
Kittiwakes	Cook Inlet	15	0.31	87	0.27
	Gulf of Alaska	113	0.24	110	0.26
	Aleutians	20	0.27	84	0.22
	Bering Sea	84	0.24	94	0.24
	Chukchi Sea	18	0.82	65	0.54
	Alaska	235	0.29	110	0.32
	Newfoundland	7	0.86	65	0.56
	Vedoy I., Norway	20	0.69	41	0.28
	Hornoya I., Norway	17	0.93	27	0.25
	Isle of May, UK	17	0.59	69	0.41
	North Sea 1986	15	1.09	29	0.32
	North Sea 1987	20	0.96	49	0.47
	North Sea 1988	21	0.61	85	0.52
	West Coast UK	31	0.62	56	0.35
	Atlantic Ocean	148	0.77	53	0.39
Murre	Cook Inlet	14	0.61	29	0.18
	Gulf of Alaska	34	0.54	34	0.18
	Aleutians	13	0.41	76	0.31
	Bering Sea	52	0.50	35	0.17
	Alaska	99	0.50	41	0.20
	California	29	0.74	29	0.22
	Newfoundland	14	0.76	9	0.07
	Isle of May, UK	21	0.78	7	0.06
	Europe	19	0.70	20	0.14
	Atlantic Ocean	54	0.75	12	0.09

(See text for sources of data).

Kittiwake breeding success measured in the Atlantic during 143 colony-years (42 colonies, 1973–2001; Birkhead and Nettleship, 1988; Harris and Wanless, 1990, unpublished data; Hamer et al., 1993; Erikstad et al., 1995; Barrett, 1996, unpublished data; Anker-Nilssen et al., 1997) averaged 0.77 ± 0.39 chicks/pair and variability (CV = 53%) was more than four times greater than that observed in Atlantic murre (12%, Table 4.4). Indeed, it appears that under a wide range of conditions, kittiwake productivity is always more variable than murre productivity (Fig. 4.41). Furthermore, for both species, variability is high when productivity (and

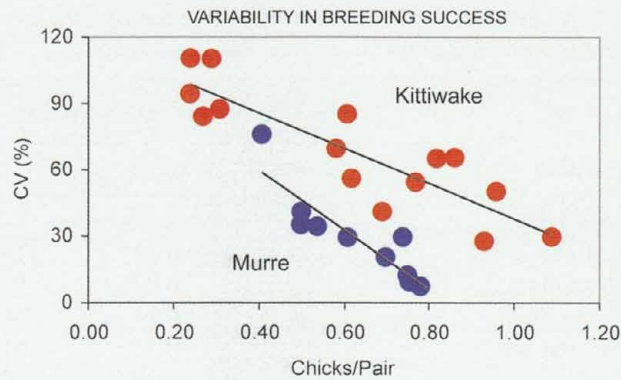


Figure 4.41: Coefficient of variation (CV) in breeding success versus average breeding success in Common Murres ($y = -134x + 114$; $r^2 = 0.79$) and black-legged kittiwakes ($y = -80.3x + 118$; $r^2 = 0.77$) among different colony-years within various regions and subregions around the world (see Table 4.4).

presumably food density) is low. This suggests that factors controlling seabird populations operate over moderate to large regional scales such as those arbitrarily selected in Table 4.4. It appears that in “good times,” high-density prey aggregations are available to most colonies in a region, most colonies do well, and variability is therefore low. In “bad times,” prey aggregations are more patchy and available to fewer colonies, more colonies fail, and variability is therefore high.

4.8.4. Population Dynamics of Seabirds in Cook Inlet

Our study was designed to provide contrasting data from a “food-poor” colony (Chisik), where murre and kittiwake populations were known to have been declining at rates of 4–9% per annum for the past 30 years (Fig. 4.42), and a “food-rich” colony (Gull), where murre and kittiwake populations grew at rates of 9% per annum at some point during the past 25 years (Zador et al., 1997; Piatt, 2002a). Kittiwakes increased rapidly on Gull Island during the 1980s, but populations leveled off in the 1990s and remained at the same level throughout the course of our study. Evidence suggests that this was due to saturation of nesting habitat on the island; otherwise, kittiwakes would still be increasing at the rate observed prior to the plateau, and at a rate similar to that observed for murres (which were not limited by nesting habitat). Trends at the Barren Islands were unknown prior to the *Exxon Valdez* oil spill, but both murres and kittiwakes exhibited modest increasing trends (Fig. 4.42) during the 1990s (Roseneau et al., 1997, 2000).

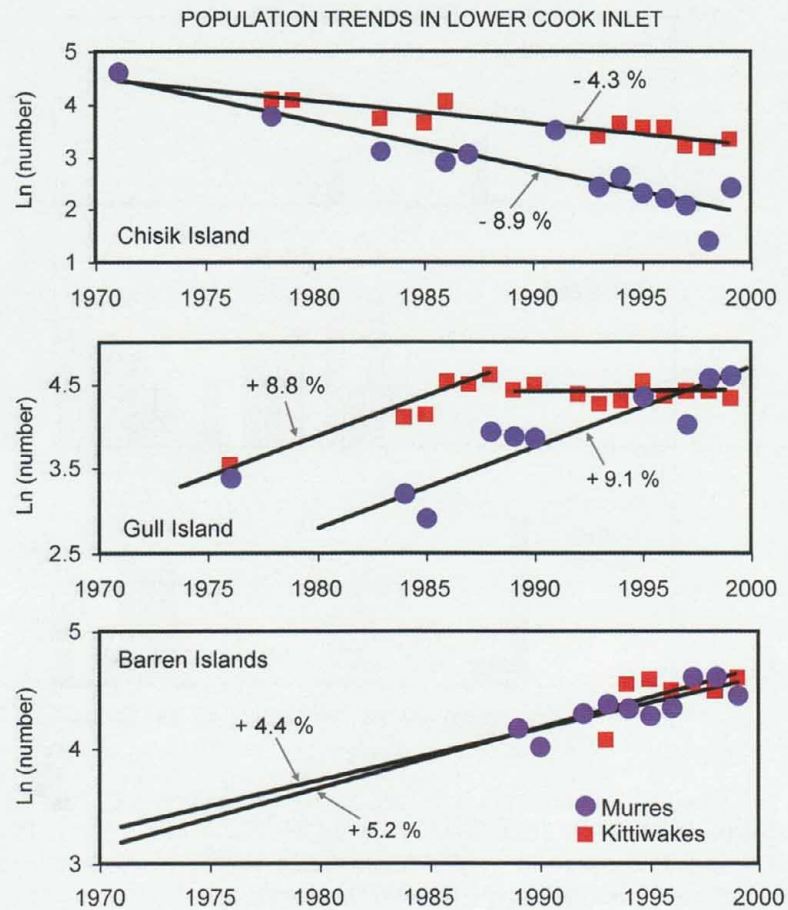


Figure 4.42: Population trends for populations of common murres and black-legged kittiwakes at Chisik, Gull, and Barren islands, with average annual percentage changes. Data for Gull and Chisik from Piatt 2002, and Zador et al., 1997. Data for Barren Islands from Roseneau et al., 1997 and Roseneau et al., 2000.

Historical measures of productivity in kittiwakes (Fig. 4.43) are parallel to population trends. Kittiwakes have failed chronically at Chisik for more than 30 years, averaging 0.05 chicks/pair during that time and only 0.02 chicks/pair during our study in 1995–1999 (Zador et al., 1999; Shultz et al., 2002). Kittiwakes averaged 0.44 chicks/pair at Gull Island since 1984 and 0.48 chicks/pair during our study. This is higher average productivity than has been observed at any other colony in Alaska except Cape Lisburne, where populations have been increasing during the past couple of

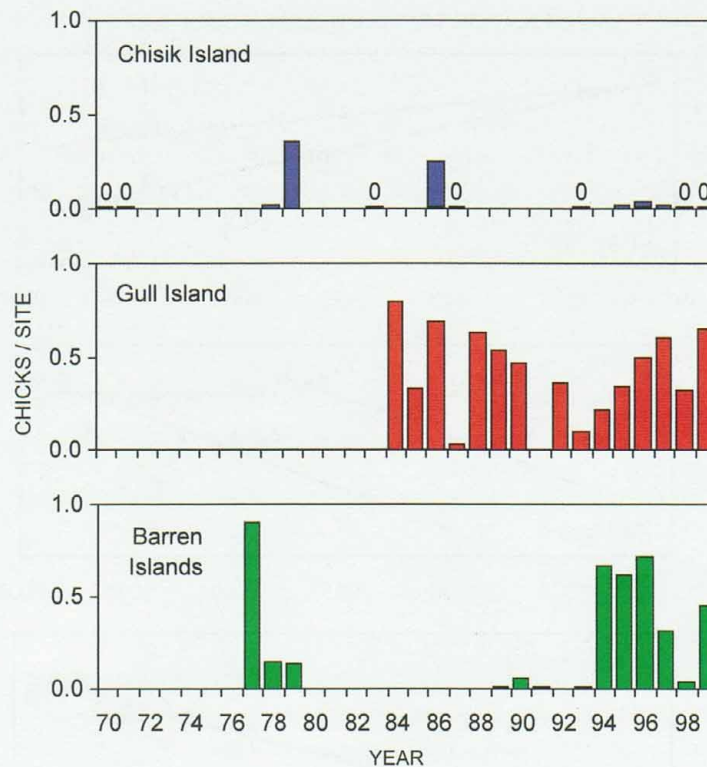


Figure 4.43: Historical productivity of black-legged kittiwakes at Chisik, Gull, and Barren islands, 1979–1999. Data from Piatt, 2002a; Zador et al., 1997; Roseneau et al., 2000 and Dragoo et al., 2000. Years when surveys were conducted but productivity was zero are indicated with a “0” above the bar.

decades (Dragoo et al., 2000). Productivity was more variable at the Barrens, averaging 0.29 chicks/pair during the past decade and 0.43 chicks/pair during 1995–1999 (Dragoo et al., 2000; Roseneau et al., 2000).

In contrast, murre productivity does not correlate with population trends. Despite having markedly different population trends at the three colonies (Fig. 4.42), breeding success was high on Chisik (average of 0.56 chicks/pair), Gull (0.54 chicks/pair), and the Barren Islands (0.73 chicks/pair) during five years of study in 1995–1999 (Roseneau et al., 2000; Van Pelt et al., 2002). There are no prior historical reproductive data for murres except from the Barrens in 1989–1993 (Nysewander et al., 1993; Roseneau et al., 1997; Boersma et al., 1995). When included, these data suggest an average productivity of 0.54 chicks/pair at the Barrens during the past 12 years.

Results from Chisik beg the question: Why is the murre population there declining by 9% per annum (pa) when reproductive success appears normal? A similar question has been asked about murres in the Shetlands, which continued to have high breeding success even as numbers at colonies declined in apparent response to a crash in food stocks (Furness and Camphuysen, 1997). Preliminary results of a survival study on Gull and Chisik islands (Piatt, 2004) may help answer this question. This study suggested that there are marked differences in population parameters of murres on Gull and Chisik islands. On Chisik, annual adult mortality (9.2% pa) exceeds slightly the rate of population decline (−8.9% pa), suggesting a small balancing rate of 0.3% pa increase due to recruitment (or possibly immigration). This indicates that survival of murre chicks to breeding at Chisik is negligible. Indeed, survival of chicks is likely to be much lower if fledgling chicks are underweight (Hatch, 1983; Sagar and Horning, 1998) – as they frequently are at Chisik (Van Pelt et al., 2002). Furthermore, recruitment at a declining murre colony is likely to be less than 20% (Hudson, 1985) and possibly less than 5% (Hatchwell and Birkhead, 1991). This would explain how Chisik murres can maintain such high breeding success and yet experience serious population declines. In contrast, the high rate (9.1% pa) of murre population increase at Gull Island can be explained by a low rate (6% pa) of adult mortality that is more than offset by high rates of recruitment and/or immigration.

Kittiwake population parameters are more straightforward (Piatt, 2004). At Chisik, recruitment has to be virtually zero because productivity is negligible. Thus, the population decline (−4.3% pa) is explained entirely by adult mortality (6.7% pa), offset slightly by immigration. At Gull Island, a much higher adult mortality rate (14.5% pa) is balanced by much higher levels of productivity, recruitment, and immigration. The differences in survival and productivity between Gull and Chisik seem to support the hypothesis that long-lived seabirds trade off the costs of reproduction with adult survival (Erikstad et al., 1998; Golet et al., 1998, 2004).

Population Parameter Indices

The question posed by the *Exxon Valdez* Oil Spill Trustee Council was whether or not recovery of seabirds was limited by environmental conditions in the Gulf of Alaska – particularly at the Barren Islands, whose murre populations were hard hit by the spill (Piatt et al., 1990; Roseneau et al., 1997). But how do we compare the robustness of seabird populations among colonies in Cook Inlet, or among regions in Alaska? As illustrated in the preceeding text, any one parameter we choose to examine may be biased depending on the form of its relationship to food supply and whether it is highly variable or relatively constant in the face of environmental change. Similarly, any one species may be more sensitive to different aspects of environmental change than another species.

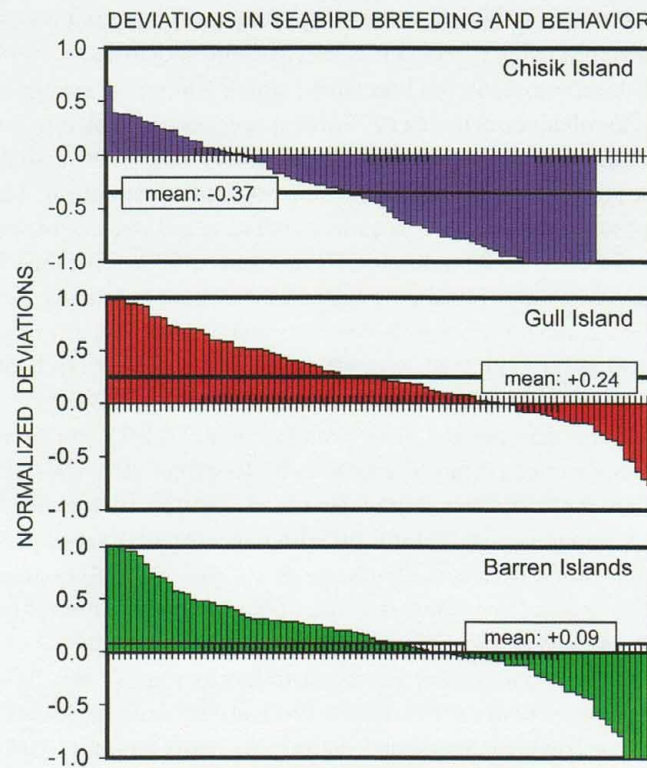


Figure 4.44: Normalized deviations from average of seabird breeding and behavioral parameters at Chisik, Gull, and Barren islands, 1995–1999. Deviations have been arbitrarily ranked by magnitude from most positive (left) to most negative (right). Data from Piatt, 2002a and Roseneau et al., 2000.

One way to assess and compare the performance of seabirds among colonies in Cook Inlet is to compare the deviation of parameter values at any one colony with the average of all three colonies combined (Fig. 4.44). For example, the average breeding success of kittiwakes in 15 colony-years (three colonies in 1995–1999) of study was 0.312 chicks/pair (Shultz et al., 2002). Success of kittiwakes at the Barrens was lower than this in 2 years of study and higher in 3 years. Success was higher than this average in all 5 years at Gull Island, and much lower than this average in all 5 years at Chisik. Similarly, we calculated deviations from average in many different behavioural, reproductive and physiological parameters (e.g., attendance, feeding rate, growth rate, fledging success, etc., for both murre and kittiwakes; from tables in Shultz et al., 2002; Van Pelt et al., 2002), standardized the deviations, and arbitrarily ranked them from largest to smallest at each colony so that we could examine them

all together (Fig. 4.44). In total, we can compare 266 parameter deviations (about 20 species parameters by year, colony, with some missing values). This provides an integrated assessment of how well seabirds were doing at each colony during the 5 years of study. Analysis reveals (Fig. 4.44) that seabirds at Gull Island do better than average most of the time (mean deviation = +0.24), while those at Chisik do poorly most of the time (mean deviation = -0.37). At the Barrens, measured parameters were above average slightly more often than they were below average (mean deviation = +0.09).

Judging from the range of parameter values we observed at Chisik and Gull islands, and in comparing these with values obtained in similar studies on murres and kittiwakes conducted elsewhere under a wide range of conditions (e.g., Hamer et al., 1993; Uttley et al., 1994; Monaghan et al., 1994; Dragoo et al., 2000; Gill, 1999 etc.), it is clear that Chisik and Gull exemplify the extremes of failing and thriving colonies, respectively, in the North Pacific and Atlantic oceans. Therefore, this analysis provides a calibration for seabird performance at the Barren Islands and suggests that murres and kittiwakes there are doing modestly well. This conclusion is corroborated by data on population trends (Fig. 4.42), and once again suggests that murre populations at the Barren Islands should not be limited by food in their recovery from the oil spill.

Indeed, there is a strong correlation between our indices of population health and observed population trends (Fig. 4.45). This relationship seems intuitively obvious. Our parameter indices integrate a suite of values that include behavioral, physiological and biological measurements. The combination of these parameters – and many more unmeasured parameters – is ultimately what determines whether a population

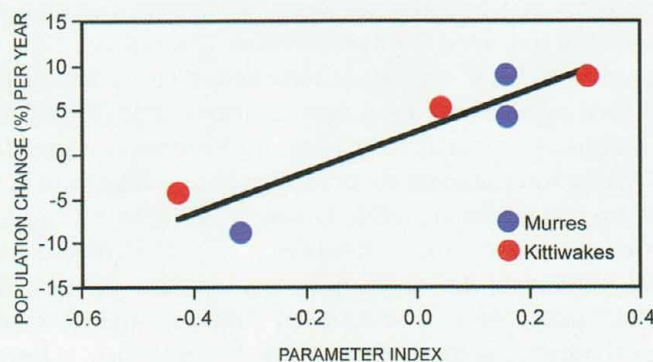


Figure 4.45: Average parameter index (from Fig. 4.44) versus population trend (from Fig. 4.42) for common murres and black-legged kittiwakes at Chisik, Gull, and Barren islands.

will increase or decrease. Similarly, population trend represents an integration of all factors influencing population biology.

The parameter index also offers an instantaneous measure of the health of seabird populations, whereas population trend data, by definition, needs to be collected over many years to establish a trend. One year's sampling may be all that is needed to assess the status of populations (e.g., parameter indices for any one year in 1995–1999 at Chisik were always negative, ranging from -0.24 to -0.62 ; whereas at Gull they were always positive, ranging from $+0.19$ to $+0.29$). In contrast, census data can be highly variable among consecutive years, and may need to be collected for a decade or longer to establish trends (Dragoo et al., 2000). Finally, census information will be misleading if study plots used for census purposes become saturated with breeding birds, or breeding habitat on a colony is saturated (as we observed on Gull Island, see "Population Dynamics" above).

4.8.5. Long-term Changes in the Gulf of Alaska Marine Environment

Are environmental conditions in lower Cook Inlet typical of those found elsewhere in the Gulf of Alaska or Bering Sea? In the absence of quantitative long-term data on food supplies, one way to answer that question is to compare seabird parameter indices from Cook Inlet to those gathered in other areas of Alaska. Unfortunately, the full suite of parameters measured in our studies has rarely been surveyed at other colonies. However, one parameter that has been widely reported is breeding success of black-legged kittiwakes (Table 4.4). We have established that kittiwake breeding success exhibits a strong, sigmoidal response to prey density (Fig. 4.39) and from that quantitative relationship we also know that kittiwake breeding success above 0.46 chicks/pair represents asymptotic reproduction unlimited by food supply, while breeding success below 0.015 chicks/pair represents asymptotic failure to reproduce under conditions of severe food deprivation (Piatt, 2002a). Breeding success that ranges between 0.015 and 0.46 chicks/pair represents reproduction that is limited to some degree by food supplies that hover around the threshold (Piatt, 2002a).

Using these criteria, we can indirectly assess the historical status of food supplies for seabirds in Alaska by examining the breeding success of kittiwakes in past years (Fig. 4.46, data from Hatch et al., 1993; Dragoo et al., 2000). Prior to the regime shift that occurred in the late 1970s (Francis et al., 1998), kittiwake productivity in both the Gulf of Alaska and Bering Sea was very similar: only a small proportion (5–6%) of colony-years were food-deprived failures, slightly more than half (55–56%) were limited to some degree by food supply, and a large proportion (38–40%) were unlimited by food. After the regime shift, but mostly prior to the *Exxon Valdez* oil spill in 1989, there was a marked change in kittiwake productivity (Fig. 4.46). The frequency of food-deprived failures in the 1980s increased six-fold

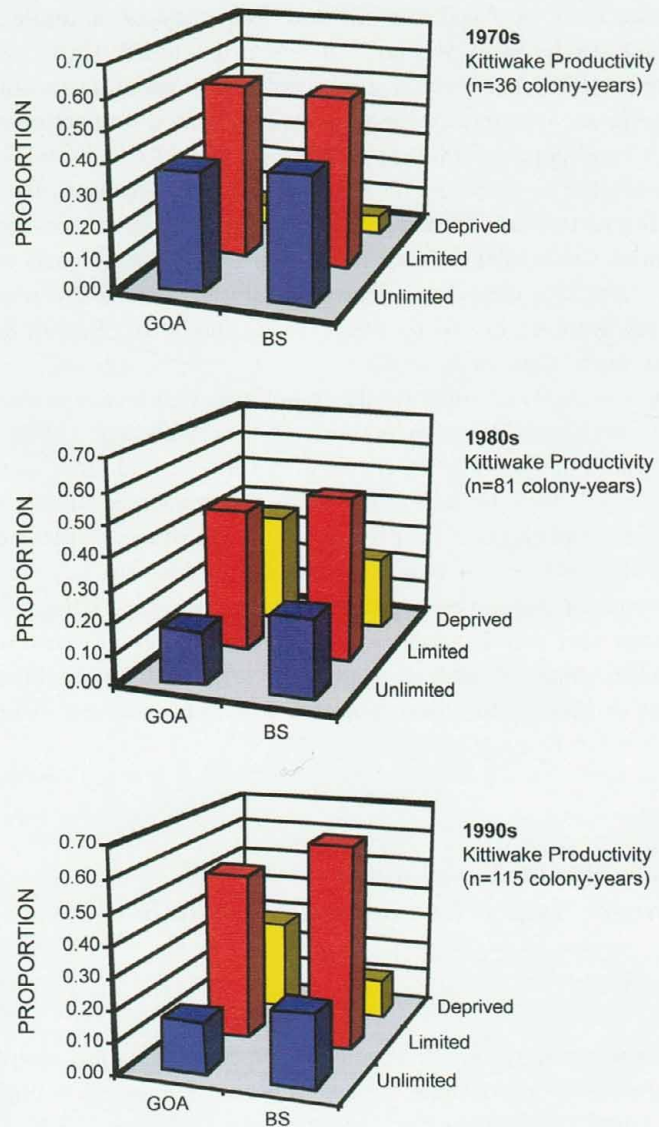


Figure 4.46: Historical breeding success (brs) of black-legged kittiwakes in the Gulf of Alaska (GOA) and Bering Sea (BS), categorized by functional relationships with food supply as "Deprived" (brs <0.015 chicks/pair), "Limited" (0.015 brs <0.46 chicks/pair), and "Unlimited" (brs >0.46 chicks/pair). Data from Hatch et al., 1993, Zador et al., 1997, Dragoo et al., 2000, and Roseneau et al., 2000.

(to 37%) in the Gulf of Alaska, while the frequency of unlimited production declined by half (to 17%). A similar, but less pronounced, shift occurred in the Bering Sea. In the 1990s, there was a significant improvement in feeding conditions in the Gulf of Alaska; whereas the frequency of unlimited production remained the same (at 17%), food-deprived failures decreased from 37 to 30% while production that was food-limited to some degree increased from 46 to 54%. By comparison, however, conditions in Cook Inlet had improved substantially more than the Gulf as a whole (in which Cook Inlet data are included). Of 24 colony-years of production in the 1990s, only 21% were food-deprived failures, 50% were limited to some degree, and 29% were unlimited by food. Conditions in the Bering Sea improved even more than in the Gulf of Alaska.

In summary, this analysis supports the hypothesis that a regime shift in the late 1970s reduced food availability to seabirds in the 1980s and 1990s, resulting in widespread population declines, lower breeding success, and mass mortality events (Piatt and Anderson, 1996; Francis et al., 1998). The evidence further suggests that there was a slight improvement in feeding conditions in the 1990s and that conditions in Cook Inlet are better than those in the Gulf as a whole. In general, however, current conditions continue to be depressed compared to the 1970s. While seabirds in Cook Inlet colonies may have already recovered numerically to levels observed prior to the *Exxon Valdez* oil spill, it is still not clear whether conditions elsewhere in the Gulf of Alaska would have supported similar rates of recovery during the 1990s.

4.9. Marine Mammal Populations

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4.9.1. Harbor Seals

Harbor seals are the most widely distributed pinniped in the world, occurring in both the North Pacific and North Atlantic oceans. Their range is nearly continuous around the rim of the North Pacific from San Ignacio Lagoon, Mexico (27°N) to Hokkaido, Japan (43°N), and extends into the eastern Bering Sea as far north as Kuskokwim Bay (60°N) (Fig. 4.47). Today, there are some 36,000 harbor seals in the northern GOA between Kayak I. and the Copper River Delta in the east to False Pass at the end of the Alaska Peninsula in the west (Boveng et al., 2003). This total is much lower than in the middle of the past century because of the eradication programs and commercial harvests described in Section 3.5, and unexplained losses since the early 1970s (Fig. 4.48).